THE UNUSUAL DEFLEXED PODETIUM OF THE LICHEN *CLADONIA INCRASSATA*

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ABSTRACT. Lichens in the genus *Cladonia* are characterized by an erect, photosynthetic secondary thallus called a podetium. Growth of the podetium is influenced primarily by a meristem-like bundle of fungal tissue near the apex, which lacks direct contact with the algal host. In most *Cladonia* species the podetium, whether branched or unbranched, grows perpendicular to the growing surface and the habit of the podetium is erect. Apothecia are borne apically and they are generally upward-facing. In *C. incrassata*, vertical growth may be interrupted very early in ontogeny, resulting in mature podetia that are deflexed. In these podetia, the hymenial (spore-bearing) surface of the apothecium faces the growing surface instead of facing upward. In addition to variability of their habit, mature podetia of *C. incrassata* may be branched or unbranched. When branching occurs it is initiated by divisions of the fungal meristem, either early in ontogeny or later, as a by-product of the migration of the meristem during deflexion. Unbranched podetia are narrow, club-like structures with a more or less continuous outer layer, or they may be wide with a flabelliform-hooded habit and a deeply fissured exterior. Branched podetia resemble *C. cristatella*, which has contributed to confusion in the taxonomic literature surrounding this species.

Key Words: Cladoniaceae, growth dynamics, morphogenesis, variability

Cladonia incrassata Flörke is an inconspicuous, relatively uncommon lichen species of New England and the eastern United States. It grows on soil, stumps, and decaying wood in shady or semi-exposed habitats, and it is usually found in damp microenvironments or on substrata where moisture is perennially available. The size and growth habit of this lichen may contribute to its infrequent appearance in herbarium collections. The podetia of *C. incrassata* are generally shorter than 1 cm. The red apothecia that make species such as *C. cristatella* Tuck. conspicuous in the field are often obscured by podetial growth and deflexion in *C. incrassata*. Finally, the damp, shady habitat of this species is somewhat less accessible than that of other Cladonias. Mature specimens of *C. incrassata* are variable, and the development and gross morphology of this species are poorly understood. Mature podetia may be narrow (1–2 mm), club-like structures with an

unbroken outer surface. Frequently, mature podetia are broad ($\geq$ 1 cm), deeply fissured, hood-like structures. Instead of an erect habit, the podetium of mature *C. incrassata* is often deflexed and the apothecia face the growing surface. *Cladonia incrassata* is usually distinguished from *C. cristatella* in the laboratory on the basis of its sorediate primary thallus (squamules) and the presence of squamatic acid, rather than by the subtly articulated features of its podetium. This may explain why the deflexed habit has been overlooked in the literature.

While specimens from the eastern United States are conspecific with European material (Ahti, pers. comm.), this species is absent from western North America (Hammer 1995a, 1996a). Thomson (1968) listed three forms for *Cladonia incrassata* in North America but he did not mention its peculiar growth habit. The formae listed by Thomson reflect minor variations in mature thalli, which may be attributable to growing conditions, but which are also the result of varying rates of growth and development. Thomson also provided the synonym *C. cristatella* var. *paludicola* Tuck., which reflects the taxonomic controversy that surrounds this species in North America. The goal of this study is to describe the developmental stages that give rise to the unusual deflexed podetium of mature *C. incrassata*.

MATERIALS AND METHODS

Specimens of *Cladonia incrassata* for dissection were collected from soil and decaying wood in shady or semi-exposed habitats in Barnstable and Plymouth Counties, Massachusetts. Several hundred thalli were examined, including podetia of all developmental stages. These included immature, incipient podetia < 1 mm tall, to mature podetia > 1 cm tall. In addition, preserved specimens from North America and Europe at the Farlow Herbarium (FH) and the Tuckerman Herbarium (FH-TUCK) were examined and annotated (Table 1), and compared with *C. cristatella* (see Hammer 1997b for representative specimens of *C. cristatella*).

Longitudinal sections of freshly collected podetia were prepared for microscopy. Sections were mounted in lactophenol cotton blue (Stevens 1981) with glycerin. Photomicrographs (LM) were prepared under bright field refraction with an Olympus BHS microscope. Scanning electron micrographs (SEM) were prepared

Table 1. Representative specimens of *Cladonia incrassata* from FH and FH-TUCK examined in this study (all with deflexed podetia).

Specimen	Locality
Ahmadjian 491	Massachusetts
Evans 1308	Connecticut
Gray 1308	West Virginia
Hammer 5751	Massachusetts
Hammer 6010	Massachusetts
Luttrell 3032	Virginia
Merrill s.n.	Maine
Merrill 2097	Vermont
Riddle 382	Massachusetts
Riddle 615	Massachusetts
Robbins s.n.	Massachusetts
Tuckerman s.n.	Massachusetts (lectotype, *C. paludicola*)
Sandstede Exs. 1652	Germany
Santesson 14402	Sweden
Savicz 528	Belarus

from approximately 30 freshly collected specimens. See Hammer (1996b) for details on SEM methodology.

The descriptive terminology for lichen morphogenesis is not yet an established convention and here I use certain terminological conventions adopted in previous papers. For example, the cluster of apical cells that comprises meristem-like fungal tissue is called the "meristem" or "meristem bundle." As bundles elongate and begin to form a stipe, they are referred to as "incipient podetia." Bundles split in a characteristic fashion, producing a distinct cluster called the "meristem initial." The meristem initial refers to a developmental unit of up to five bundles that usually gives rise to branches.

RESULTS

The very early ontogeny of *Cladonia incrassata* is similar to that of other species in *Cladonia,* as described in Hammer (1995b, 1996b, c, 1997a, b). The earliest distinguishable podetial structure, which is ca. 100 μm tall, is exclusively fungal (Figure 1). In earliest ontogeny it is a roughly spheroid structure comprised of irregularly arranged meristematic tissue, which gives rise to all of the subsequent fungal tissue of the podetium. The podetium is a solid mass of cells at this early stage, and
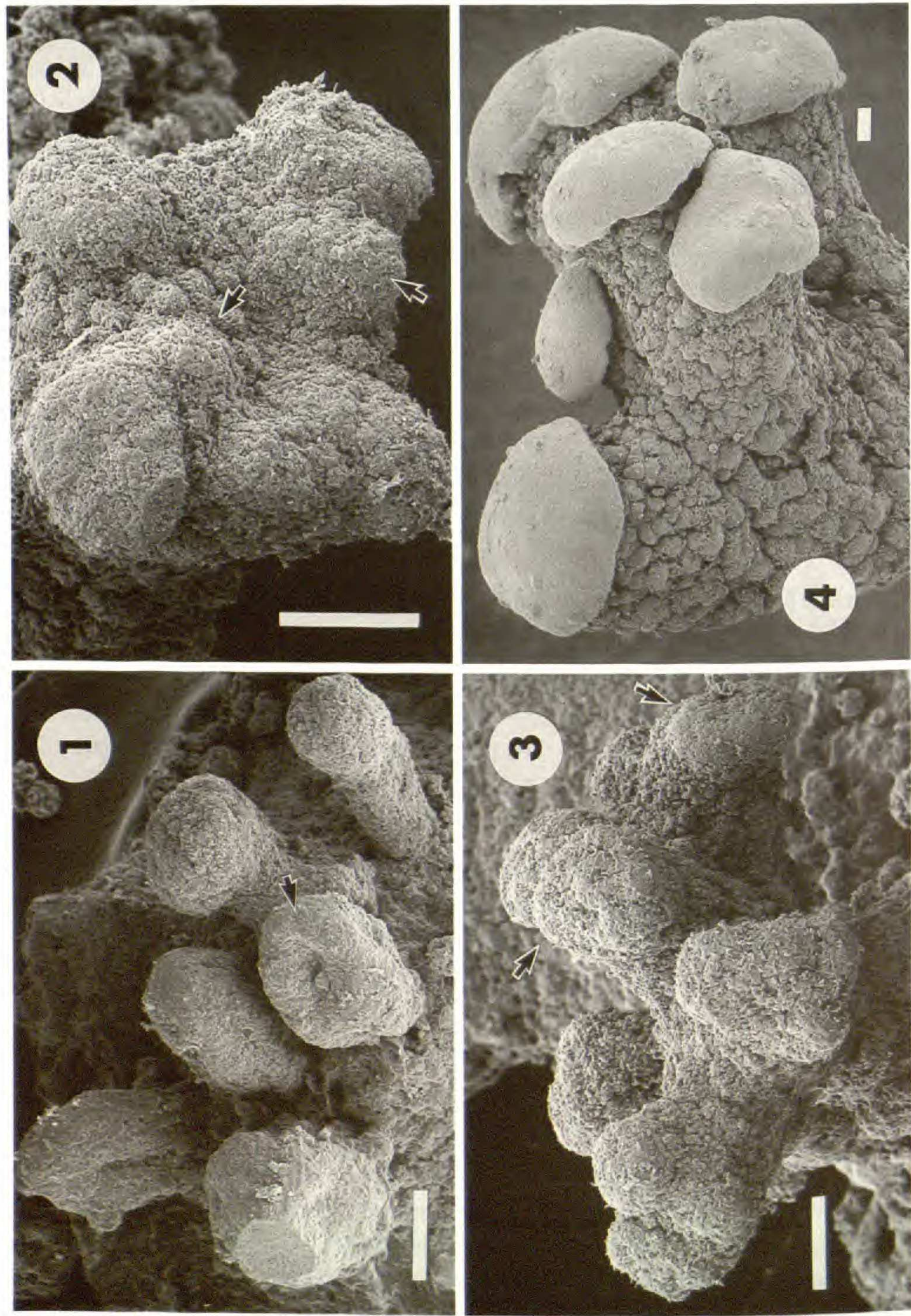
internal lacunae, which are a by-product of growth and elongation, have not developed. As the structure elongates, the cells of the lower portion assume a vertical orientation, generally growing perpendicular to the substratum. The upper portion of the podetium, which is distal to the substratum, widens, and the cells in the upper ½–⅓ of the podetium are oriented in a radial conformation. As development continues, the upper portion of the podetium remains solid and lacunae develop below. A layer of algal cells develops toward the base of the podetium, which is eventually distinguishable as a stipe. The upper (fungal) portion of the podetium grows wider than the supporting stipe, which is composed of both fungal and algal cells. The upper portion, which remains meristematic at this stage, usually does not exceed 100 μm diam. until it divides. During early ontogeny podetium elongation and meristem widening and division can occur independently of one another (Figures 2 and 3).

The earliest divisions of the meristem follow roughly the pattern described for *Cladina subtenuis* (Abb.) Hale & Culb. (Hammer 1997a) and *Cladonia cristatella* (Hammer 1997b). One difference is that the meristem of *C. incrassata* may divide at the surface of the squamule at a very early stage, before elongation of the podetium, as well as later, on maturing podetia. Division of the meristem can be interrupted at any stage, or it may follow through to the completion of a five-part meristem initial (see Hammer 1996d), which is formed by a series of four divisions

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Figures 1–4.   Early bending and branching in *Cladonia incrassata* (SEM). 1. Cluster of meristem bundles (incipient podetia) in early stages of ontogeny. Note two right-hand structures, whose apices are bent toward the left. Rim of one bundle has begun to grow differentially (arrow). Differential growth and deformation further advanced in bundle in upper left. Further widening and meristem division (see next figure) could occur in similar bundles. 2. Top view of very early division of meristem, slightly later in ontogeny than previous figure. Bundles are forming a five-part meristem initial, reminiscent of *C. cristatella*. Arrows indicate secondary divisions forming from bundles. 3. Side view of meristem initial derived from a single bundle. Slightly later in ontogeny than previous figure. Bundles face sideways or downward (arrows) and subsequent branching follows this growth pattern. 4. Maturing apex of podetium. Note orientation of four right-hand bundles and incipient branches that bear them. Two left-hand bundles are still vertically oriented. Scale bars = 100 μm.
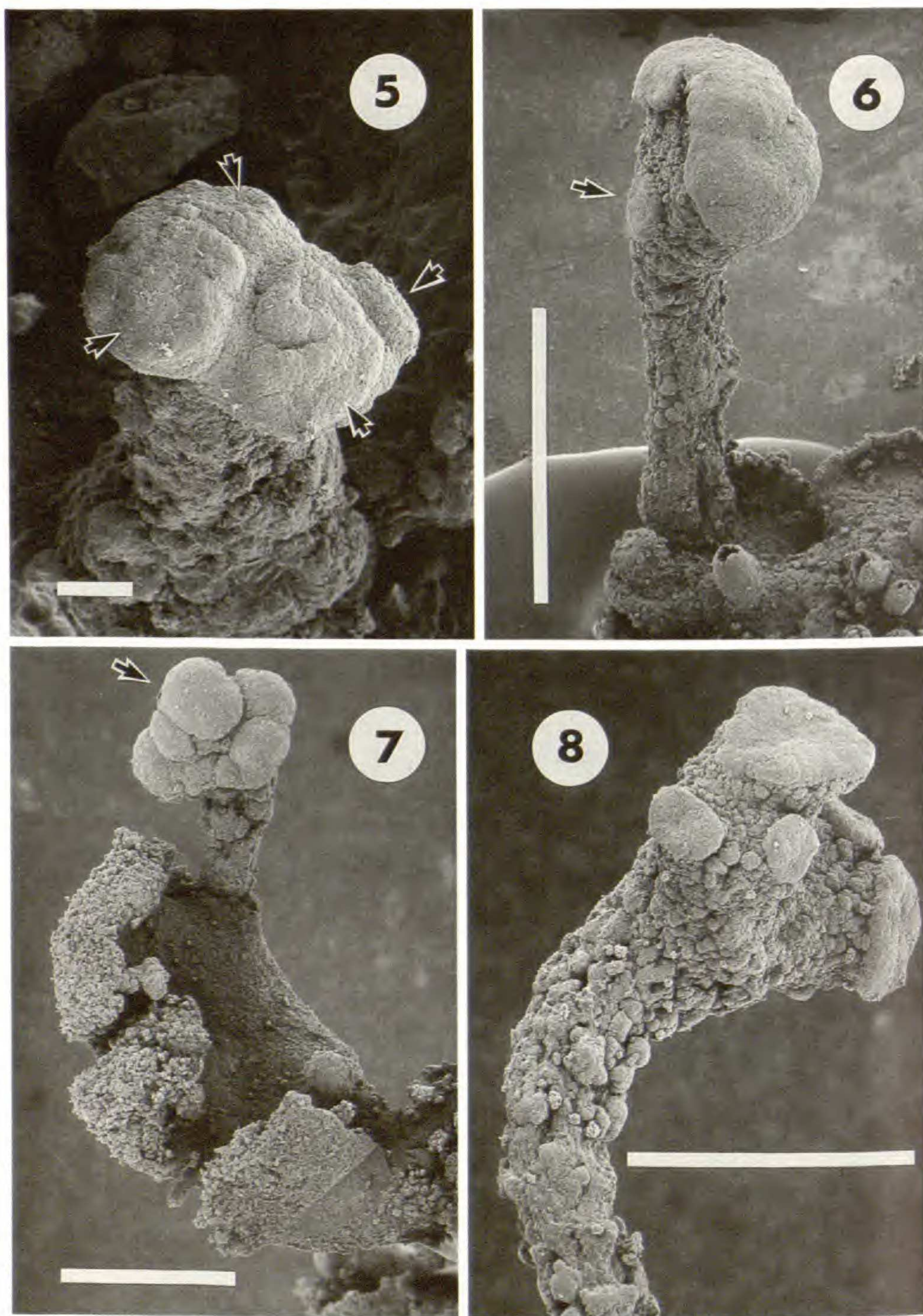
Figures 5–8.   Early ontogeny and podetial elongation of *Cladonia incrassata* (SEM). 5. Fungal apical meristem in early stage of podetial development. The meristem has begun to split into four distinct regions (arrows). 6. Podetium later in ontogeny. Meristem has migrated upward and is positioned obliquely at apex of podetium. Arrow indicates portion of meristem left behind (on future adaxial surface), which will later form a new branch on the podetium. Note pycnidia near base of podetium. 7. Maturing, deflexed podetium growing from end of squamule. Meristem has begun to split. Largest

of the fungal tissue (Figure 2). The tissue beneath any portion of the meristem initial may grow vertically at any stage (Figure 3), independent of the other meristem bundles. Bundles that continue to divide may form separate podetia or irregularly branched podetia. Alternatively, their growth may be synchronized as branches on one podetium (Figure 4), which resembles *C. cristatella* at maturity.

Generally, the podetium of *Cladonia incrassata* elongates in early growth stages (Figures 5 and 6) and the meristem divides as ontogeny progresses (Figure 7). As the podetium elongates, the (usually undivided) fungal meristem grows asymmetrically, appearing to be pushed to one side of the axis of growth by the underlying tissue (Figure 6). As the fungal meristem migrates (or is pushed) upward and sideways, portions of it may split off and remain isolated on the opposite side of the axis of vertical growth. This isolated meristem tissue (Figure 6) can later form branches that arise from the adaxial side of the deflexed podetium. As deflexed growth continues, most of the fungal meristem is borne abaxially, facing the substratum (Figures 7 and 8). The partially divided meristem may split into separate bundles or the meristem may continue to widen, resulting in irregular openings on the abaxial surface near the apothecium. In some cases the meristem divides indefinitely, producing a roughly cerebriform mass of apothecial tissue at maturity.

Mature podetia of *Cladonia incrassata* may be deeply fissured, a characteristic that is partly determined by meristem growth very early in ontogeny (Figures 9 and 10). As the meristem widens and splits (Figures 11 and 12), the cells diverge in a flabellate orientation (Figures 13–15). The fungal meristem tissue determines the first fissures, which continue to form once the algal layer develops. The widening apothecium, which is borne on the abaxial side of the podetium, develops from a band of dark-staining cells that is found directly beneath the hymenium (Figures 14–16). These cells continue to divide, while the

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portion of meristem (arrow) is near apex of the podetium. Note soredia on upturned surface of squamule. 8. Branch initiation late in ontogeny. Meristem bundles have split and most face sideways or downward. Subsequent elongation of thallus under meristem tissue will produce branches. Scale bar in Figure 5 = 100 μm; other scale bars = 1 mm.
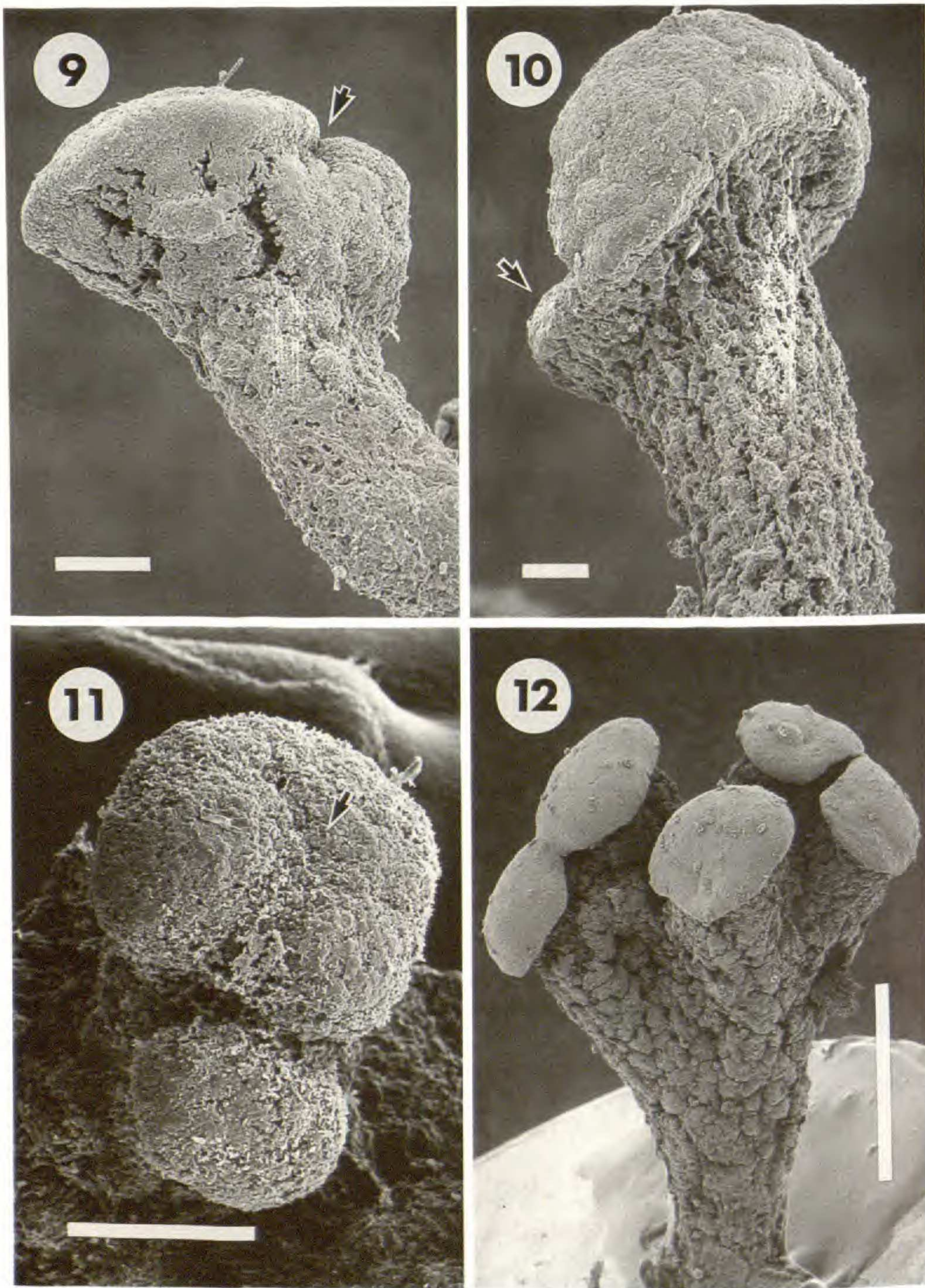
Figures 9–12. Growth patterns in *Cladonia incrassata* (SEM). 9. Early ontogeny of podetium. Interior of podetium at this stage is solid. Longitudinal fissures have begun to form and apical meristem has begun to divide (arrow). 10. Slightly later ontogeny of podetium, side view. Note large, oblique upper portion of meristem with smaller portion below to the left (arrow). 11. Front view of meristem in previous figure. Note incipient division on upper portion of meristem (arrow). 12. Maturing podetium with side branches slightly deflexed away from camera. Note that the meristem bundles have not completely

cells beneath them apparently do not continue to divide. Once the meristem has moved to the abaxial position all of the cells distal to it, including those on the opposite (adaxial) surface of the podetium, appear to stop dividing. This results in widening and proliferating fissures that make the podetium appear hood-like macroscopically.

DISCUSSION

Many of the features of the mature podetium in *Cladonia incrassata* are laid down early in ontogeny by a meristem-like mass of fungal tissue. As the meristem grows, the orientation of its cells (irregular, parallel, or radial) changes. The conformation of the meristem tissue (divided or undivided) and its position on the podetium (adaxial, apical, or abaxial) also change. The rate of change for all of these conditions differs among podetia and one result is macroscopic variability. Yet the earliest ontogeny of *C. incrassata,* like other Cladonias, follows a distinct pattern. The unusual developmental morphology of *C. incrassata* can be traced to early meristem development, with variability arising throughout ontogeny.

The source of this variability may have a genetic basis. Like the variable *Cladonia cristatella, C. incrassata* is fertile. In both species, the hymenium is well developed and abundant ascospores are common in mature specimens. Thus, the variable growth dynamics of *C. incrassata* may be the result of a heterogeneous gene pool in which recombination is frequent. While sexual processes in *Cladonia* have not been convincingly documented (see Hammer 1993), *C. incrassata* does appear to produce ascogenous cells such as those illustrated by Jahns (1970). We may infer from this that *C. incrassata* undergoes some sort of sexual reproduction, which may be reflected in developmentally based variation. It is, however, important to note that sexuality in lichens, and particularly the Cladoniaceae, is poorly understood. For example, in spite of specialized cells such as asci and ascospores that he observed in lichens, Hale (1974) was cautious

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split. Podetium resembles *C. cristatella.* Scale bar in Figures 9–11 = 100 μm; Figure 12 = 1 mm.

about attributing their presence to full sexual function. Rather, he attributed their presence to what he called "homomictic plasmogamy," a form of self-fertilization. Other authors, for example Henssen (1981), documented ascomycete sexual processes in lichens, including some *Cladonia* species, but acknowledged that those findings were contradictory.

Variability in the deflexed podetium of *Cladonia incrassata* may be attributable to environmental conditions. For example, deflexion could be a phototropic response. It might also be related to moisture availability. The effectiveness of close range spore dispersal may also be affected by downward-facing apothecia. However variable, the deflexed habit seems to be constant in this species. Specimens from eastern North America and Europe (see Table 1), which represent most of the geographical range of this species, show deflexed growth. Whatever its origin, variability is present in *C. incrassata,* and it has led to confusion in the taxonomic literature surrounding this species.

Confusion arose in the nineteenth century when Tuckerman (1882) described a "reduced form" of *Cladonia cristatella* from New England, which he named var. *paludicola.* Tuckerman was aware of *C. incrassata,* to which he also compared the new variety, stating it "corresponds closely." The basis of his statement is unclear, as *C. cristatella* and *C. incrassata* are morphologically distinct. Tuckerman may not have considered the primary squamules an important character, but the squamules of *C. incrassata* are always sorediate while those of *C. cristatella* are esorediate. Tuckerman may have studied only developing specimens that had not become sufficiently deflexed, or he may not have considered this unusual habit as a distinguishing characteristic. He may have

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Figures 13–16.   Longitudinal sections of podetia of *Cladonia incrassata* (LM). Figures show very early growth with developing hymenium borne apically or laterally. 13. Early ontogeny of podetium. Note two developing apical regions. Smaller region (arrow) will form adaxial branch after larger region grows toward right and downward. Dark band surrounding developing regions is layer of rhodocladonic acid. 14. Early deflexed growth (growing toward left). Hymenium has not formed. Meristematic cells concentrated in band indicated by arrow. Note developing lacunae (l) and algal cells (a). 15. Later deflexed growth (toward left). 16. Developing hymenium with presumed ascogenous cells (arrow). Scale bar in Figures 13–15 = 50 μm; Figure 16 = 10 μm.
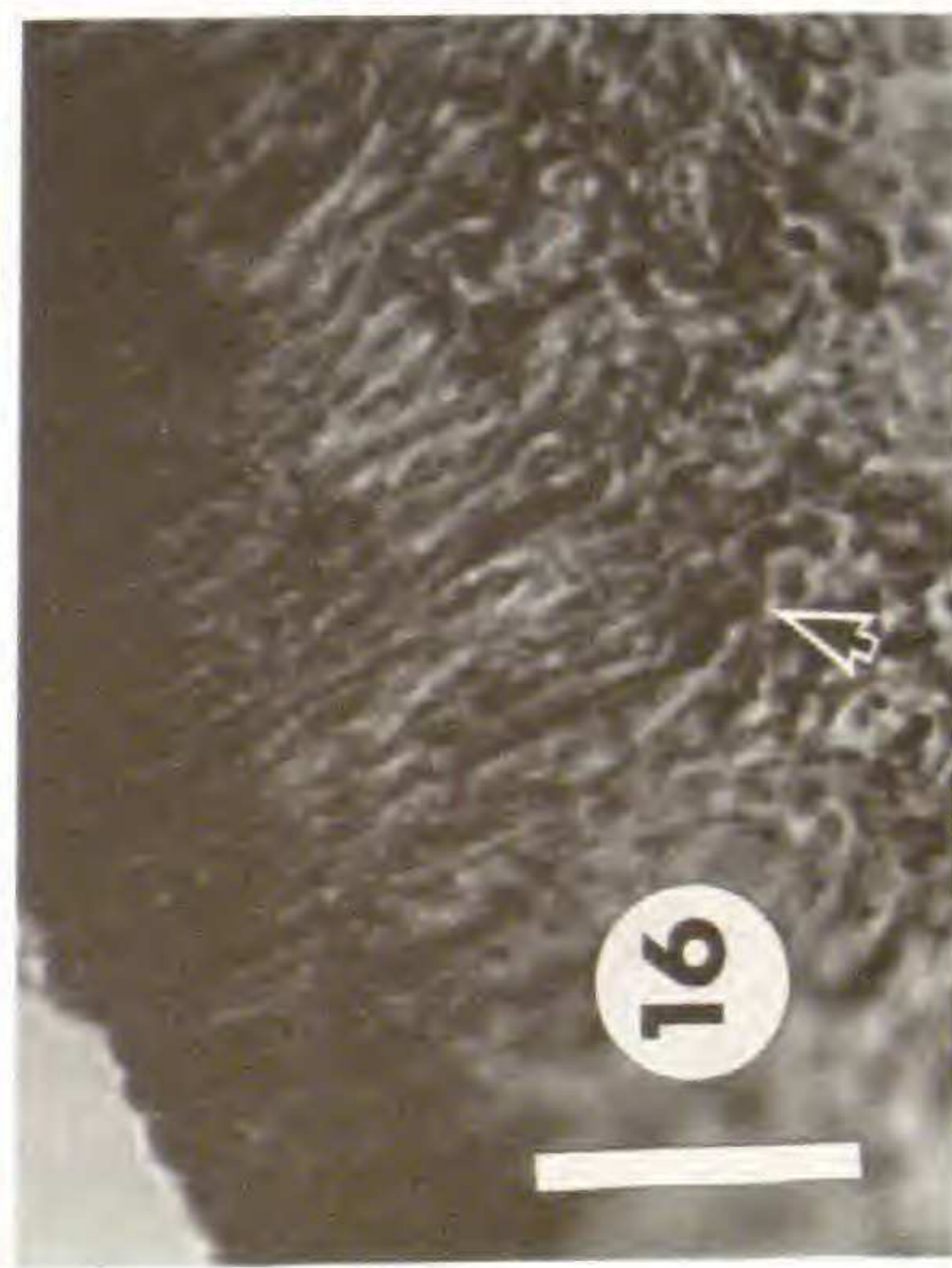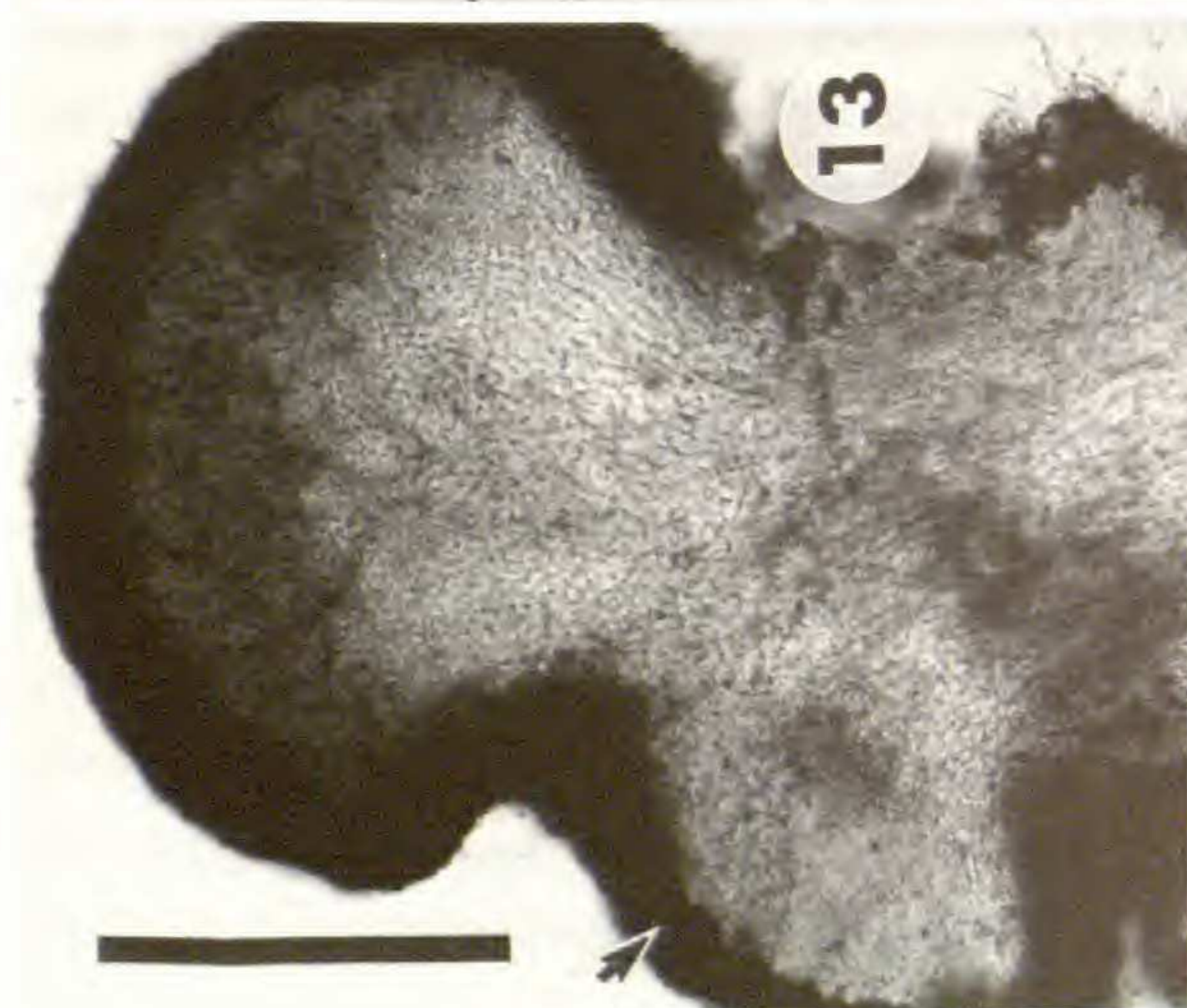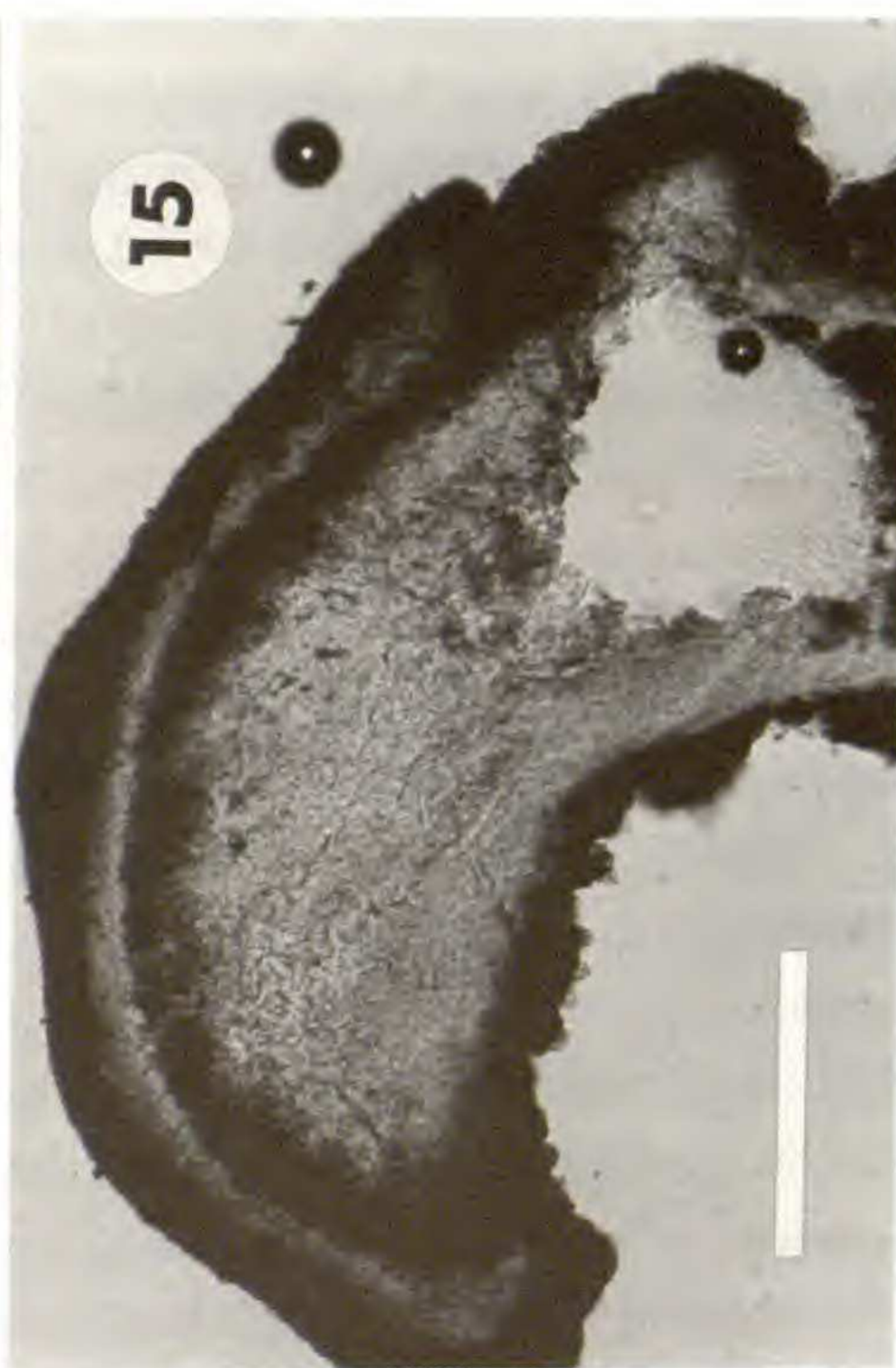
considered the "reduced" deflexed podetia as somehow atypical of the species. Deflexion in *C. incrassata* is sometimes subtle and it may become apparent late in ontogeny. Podetia at all stages that are not strongly deflexed may be confused for *C. cristatella* in the absence of microchemical tests. The name *paludicola* ("a dweller in marshes," see Stearn 1966) came to be misapplied to North American specimens of *C. incrassata* through the 1930s. Much of the problem during this century can be attributed to Charles A. Robbins, an indefatigable collector and enthusiastic amateur.

In his correspondence with George Knox Merrill, Robbins expressed indignation over what he considered to be the domination of lichenology by Europeans. In a 1923 letter to Merrill (Farlow Reference Library, unpubl.) Robbins mentioned *Cladonia paludicola*, which he considered to be distinct from *C. cristatella*. He apparently did not recognize *C. incrassata* in New England, since he labeled all of his corresponding specimens as *C. paludicola*. Perhaps to shore up his concept of what he considered to be an American endemic species, Robbins began to assign formae to his specimens such as "f. *squamulosa*." He influenced Merrill, who finally recombined var. *paludicola* and elevated it to the status of species, a decision that was made on the strength of Robbins's protestations that it was distinct (Merrill 1924). Based on Robbins's findings, Merrill reported that there was "little similarity" between the new *C. paludicola* and *C. cristatella* but conceded that "transitional states" between the species could be found in "damp situations." Evans (1930) reasserted the independent status of *C. paludicola*, which he discussed at some length, and which he considered as an endemic species. He later recognized it as a variety of *C. cristatella* (Evans 1938) and finally included it in synonymy (Evans 1944), while maintaining *C. cristatella* and *C. incrassata* as distinct species. There is no record in the literature as to the basis of Evans's decision to finally exclude *C. paludicola*, but it is noteworthy that Sandstede labeled a North American specimen (*Exsiccatum* 1684) as *C. incrassata*. It seems that Sandstede's conservative view was the most appropriate, since mature *C. incrassata* possesses a wide range of morphological variability.

Cladonia incrassata traditionally has been classified within sect. *Cocciferae* (Del.) Matt. on the basis of its red hymenium, which contains the pigment rhodocladonic acid. This convention

has been accepted since Vainio (1887, 1894, 1897), but it is based solely on the color and secondary chemistry of the podetium, without considering other characters. Choisy (1928) expressed reservations about the use of rhodocladonic acid in a natural classification of *Cladonia*. He considered developmental morphology when he rejected the monophyly of the *Cocciferae,* which he considered to be a polyphyletic, ancestral group. *Cladonia incrassata* shares certain morphological characteristics with other species in sect. *Cocciferae,* but some of these characteristics are widespread. For example, early branch initiation in this species is similar to that of *C. cristatella* although both are similar to species in sect. *Perviae* (Del.) Matt. and *Cladina* Nyl. (Hammer 1997a, b). The characteristic pattern of branch initiation is thus shared by species in various sections of *Cladonia,* and can be considered as plesiomorphic. Jahns and Beltman (1973) included *C. incrassata* with many taxa outside of sect. *Cocciferae* when they categorized its developmental morphology as "Type II," in which ascogonia are formed at the top of mature podetia. However, they hesitated to use this feature as a tool for classification. Rather, they invoked "variability" to explain how developmental morphology in *Cladonia* crossed taxonomic boundaries, an explanation that recalls Krabbe (1891), who considered *Cladonia* as a "polymorphic" group. Unfortunately, these biases have hindered the development of a natural classification for the Cladoniaceae. Variation in this important lichen group needs to be reconsidered (Hammer 1996b), and we must consequently be prepared to reconsider the established classification system in the family.

The developmental morphology of *Cladonia incrassata* suggests its placement outside of sect. *Cocciferae.* For example, the fissured podetium and indeterminate meristem of *C. incrassata* may link it to species in sect. *Helopodium* (Ach.) Matt. The five-part meristem initial in this species may be homologous to similar structures in sections *Perviae* and *Unciales* (Del.) Ahti, and the genus *Cladina* Nyl. (see Hammer 1996b, 1997a, b). Growth dynamics in *C. incrassata* suggest affinities that lie beyond *Cladonia,* suggesting an outgroup with which to compare the genus. For example the deflexed habit, which is rare or subtly expressed in other *Cladonia* species, characterizes the genus *Thysanothecium* Mont. & Berk., an endemic genus in temperate Australia and New Zealand. An outgroup such as *Thysanothecium* may

provide a useful basis for phylogenetic inferences in *Cladonia*. Understanding the evolution of morphological characters in this difficult group will provide the groundwork for a natural classification in the Cladoniaceae.

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